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Global stabilization and regulation in predator-prey models

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1 Introduction

Predator-prey models in continuous time have generally been variations of either the classical Lotka-Volterra model or its standard generalizations derived by Rosenzweig and MacArthur. These two type of models describe predator-prey interactions in nature most basically but, as conventionally interpreted from an ecological point of view, have some problem with oscillations that can bring predator/prey populations to the brink of extinction. However, many natural predator-prey populations persist stably. This gap between nature and its model prediction suggests that our insight is not enough to understand mechanisms acting in nature which stabilize population dynamics. To resolve the gap, theoreticians and experimentalists have made a long list of such processes (see, for example, [6, 12, 16, 17, 19]).

In this paper, we present some additional factors that stabilize or regulate those models. For the Lotka-Volterra model, predators or prey receiving a special type of environmental fluctuations are discussed and then a unique interior equilibrium is shown to be globally asymptotically stable if their fluctuations are bounded and weakly integrally positive. This global stabilization, in particular, can be realized even by nonnegative functions that make the limiting system structurally unstable. For a Rosenzweig-MacArthur model, we take into account constant immigration of prey as a simplest type of spatially interacting populations. A clear formulation to representing the effect of prey immigration is established by necessary and sufficient conditions derived for both the uniqueness of limit cycles and the global asymptotic stability of an interior equilibrium. From these results, the prey immigration is shown to globally stabilize or regulate predator-prey interactions.

2 For the Lotka-Volterra model

Consider

$$\begin{aligned}x' &= c(1 - e^{-y}), \\y' &= -a(1 - e^{-x}),\end{aligned}\tag{2.1}$$

where the prime denotes d/dt and parameters a, c are assumed to be positive. This system has a single equilibrium point $(0, 0)$, which is a center, i.e., a "neutrally stable" equilibrium surrounded by a family of periodic orbits whose amplitudes depend on the initial data because of a conserved quantity $V(x, y)$ given as

$$V(x, y) = a(e^{-x} + x - 1) + c(e^{-y} + y - 1).$$

The importance of these properties is the fact that (2.1) has relevance to a biological problem. By the transformation

$$x = -\log(bP/a) \quad \text{and} \quad y = -\log(dN/c)$$

for positive constants b and d , (2.1) is reduced to the classical Lotka-Volterra model well-known as the origin of theoretical study on predator-prey systems in mathematical ecology:

$$\begin{aligned}N' &= (a - bP)N, \\P' &= (-c + dN)P.\end{aligned}\tag{LV}$$

This transformation is a one-to-one correspondence from the first quadrant $Q \stackrel{\text{def}}{=} \{(N, P) : N > 0 \text{ and } P > 0\}$ to the whole real plane $\{(x, y) : x \in \mathbb{R} \text{ and } y \in \mathbb{R}\}$. The interior point $(c/d, a/b) \in Q$ corresponds to the origin $(0, 0) \in \mathbb{R}^2$. Here N and P represent the prey and predator population densities, respectively. Correspondingly to (2.1)'s properties mentioned above, (LV) has a single interior equilibrium point $(c/d, a/b)$, which is also a center surrounded by a family of periodic orbits whose amplitudes depend on the initial population sizes. This implies that the population state once changed by an external factor cannot return to the original one. Besides, the slightest change to the (LV)'s structure typically results in qualitatively different behavior (see [8]). This structural instability is often criticized because it is desirable that models describing periodical population behavior observed in nature involve robust properties such that population states strayed away from the orbit will return to the original orbit as time passes. In fact, predator-prey systems in nature apparently persist stably (in spite of being affected by external factors).

In connection with such an ecological aspect, it is significant to find out additional factors that can stabilize the origin $(0, 0)$ for (2.1). For this problem, we consider an

additional factor $-\xi(t)(1 - e^{-y})$ with a nonnegative function $\xi(t)$ to the right-hand side of the second equation of (2.1), that is,

$$\begin{aligned} x' &= c(1 - e^{-y}), \\ y' &= -a(1 - e^{-x}) - \xi(t)(1 - e^{-y}), \end{aligned} \tag{E}$$

and clarify a class of nonnegative functions $\xi(t)$ in which the origin is globally asymptotically stable (cf. [26]). Our main result is the following:

Theorem 2.1. *Suppose that $\xi(t)$ is bounded and nonnegative for $t \geq 0$. If $\xi(t)$ is weakly integrally positive, then the origin is globally asymptotically stable for (E).*

We say a nonnegative function ϕ is *weakly integrally positive* if

$$\int_I \phi(t) dt = \infty$$

for every set $I = \bigcup_{n=1}^{\infty} [\tau_n, \sigma_n]$ such that $\tau_n + \delta < \sigma_n < \tau_{n+1} \leq \sigma_n + \Delta$ for some $\delta > 0$ and $\Delta > 0$. A simple example of weakly integrally positive function is $\sin^2 t$, $1/(1+t)$, or $\sin^2 t/(1+t)$ (see [9, 10, 11, 23, 24, 25]). It is easy to see that the family of weakly integrally positive functions includes certain nonnegative functions which converge to 0 as $t \rightarrow \infty$; e.g., it includes the decreasing functions with this property. In particular, mathematically surprising thing is that the global stabilization was shown to be realized even by nonnegative functions $\xi(t)$ which converge to 0, despite the fact that the limiting system is (2.1).

Special cases of these results also contribute to the above-mentioned ecological problem of stabilizing the Lotka-Volterra model (LV). Let $\xi(t) = ch(t)/d$, where c, d are positive constants and $h(t)$ is a nonnegative and continuous function for $t \geq 0$. Then, by the same transformation mentioned above, $x = -\log(bP/a)$ and $y = -\log(dN/c)$, the system (E) is reduced to a predator-prey system of the form:

$$\begin{aligned} N' &= (a + ch(t) - dh(t)N - bP)N, \\ P' &= (-c + dN)P. \end{aligned} \tag{2.2}$$

The system (2.2) is a Lotka-Volterra model with a “simplest” type of environmental fluctuations that affect a per capita growth rate and a carrying capacity for prey more strongly than for their predators. Hence, by virtue of Theorem 2.1, we have the following.

Corollary 2.1. *If $h(t)$ is bounded and weakly integrally positive, then the interior equilibrium $(c/d, a/b)$ of (2.2) is globally asymptotically stable.*

This corollary tells that the equilibrium can be globally stabilized even by environmental fluctuations which make the limiting system equal to the structurally unstable model (LV). For such a mathematical surprising fact to be suggestive ecologically as well, some technical setting of environmental fluctuations $h(t)$ (where the same $h(t)$ is put into a per capita growth rate of prey and their carrying capacity) in (2.2) must be refined and further mathematical and ecological considerations should be developed into a model with a more biologically practical scenario. This will be left for future work.

3 For a Rosenzweig-MacArthur model

A Rosenzweig-MacArthur predator-prey model is based on the assumption that the prey population grows logistically and the predator has a Holling type II functional response:

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{k}\right) - \frac{xy}{a+x}, \\ \frac{dy}{dt} &= y \left(\frac{\mu x}{a+x} - D\right),\end{aligned}$$

where x, y are the population sizes of prey and predator, respectively, r stands for the intrinsic growth rate of prey, k is the carrying capacity, The encounter rate and the saturation value of the functional response are set to 1 by a scaling. a is the half-saturation constant, μ is conversion efficiency of predator, and D is the predator death rate. All parameters are assumed to be positive. For this model, the dynamics are well known: a positive equilibrium that has stably existed when $\mu > D$ and $a(\mu + D)/(\mu - D) > k > aD/(\mu - D)$ is bifurcated at $k = a(\mu + D)/(\mu - D)$, around which a stable limit cycle emerges when $k > a(\mu + D)/(\mu - D)$. As prey carrying capacity k is increased further, this cycle brings one or both populations closer and closer to zero. For large carrying capacities the densities can reach values where natural populations would certainly go extinct (which has become known as ‘the paradox of enrichment’ [22]).

However, the oscillations observed in many data series of natural predator-prey populations are normally not as vigorous as the fluctuations predicted by mathematical models. Therefore, natural predator-prey systems must be regulated through a mechanism that is not described in the Rosenzweig-MacArthur predator-prey models. For this problem, we incorporate a simplest type of spatially interacting populations into the Rosenzweig-MacArthur predator-prey model, where the additional assumption is made that constant-

rate prey immigration occurs only outside the system. That gives the following equations:

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{k}\right) - \frac{xy}{a+x} + b, \\ \frac{dy}{dt} &= y \left(\frac{\mu x}{a+x} - D\right),\end{aligned}\tag{3.1}$$

where the prey immigration rate is given by $b \geq 0$.

For spatial predator-prey models, there have been many studies on predator-prey dynamics in a single patch with a constant input (or output) of predator/prey from outside (or to outside) the system (e.g., see [1, 2, 3, 4, 7, 14, 15, 18, 21]). Brauer and Soudack [1-4] examined the qualitative effects of constant-rate stocking of either or both species in a general type of predator-prey system, where the asymptotic behavior of such systems and the domains of attraction for stable equilibrium states were discussed. They also investigated the change in the nature of equilibria as harvesting and stocking rates change, which was extended by Myerscough *et al.* [18] to obtain a much more comprehensive overall picture of predator-prey populations for the Rosenzweig-MacArthur model with constant rate harvesting and stocking. Also, Li [14, 15] obtained sufficient conditions on the global asymptotic stability of a positive equilibrium and the uniqueness of limit cycles for (3.1) (which were also discussed for the model derived by replacing a Holling type II functional response with a Holling type III one in (3.1)). However, most of studies are concerned only with local analysis around a positive equilibrium and solution behaviors in bifurcations, or with deriving sufficient conditions on global stability or the uniqueness of limit cycles in their systems. Therefore, the effects of spatial elements on the regulation of populations remain unclear. In our paper [27], we give necessary and sufficient conditions on both the global asymptotic stability of a positive equilibrium and the uniqueness of limit cycles for (3.1), by which it is fully clarified mathematically (not by numerical works) how the prey constant immigration dampens the large amplitude of the fluctuations emerging around a positive equilibrium. We introduce the result here.

Set

$$\Omega = \{(x, y) : x > 0 \text{ and } y > 0\}.$$

From the vector field of (3.1), we see that all the solutions starting with $x(0) > 0$, $y(0) > 0$ are bounded and remain in Ω for all future time. System (3.1) has a boundary equilibrium $E_+(k/2 + c, 0)$, where $c = \sqrt{(k/2)^2 + bk/r}$. The origin can be an equilibrium of (3.1) only when $b = 0$. Let

$$\lambda = \frac{aD}{\mu - D}.$$

If

$$\mu \leq D \quad \text{or} \quad k \leq \frac{r\lambda^2}{r\lambda + b},$$

then no equilibria exist in Ω , which implies that system (3.1) has no limit cycles. On the other hand, if

$$\mu > D \quad \text{and} \quad k > \frac{r\lambda^2}{r\lambda + b}, \quad (3.2)$$

then an interior equilibrium $E^*(\lambda, \nu)$ appears in the first quadrant, where

$$\nu = \frac{\mu}{D} \left\{ r\lambda \left(1 - \frac{\lambda}{k} \right) + b \right\}.$$

System (3.1) does not always have a limit cycle even if the positive equilibrium E^* exists. In fact, as shown in the following result, there are no limit cycles for k close to $r\lambda^2/(r\lambda + b)$.

Theorem 3.1. *If*

$$\mu > D \quad \text{and} \quad k \leq \lambda,$$

then system (3.1) has no limit cycles in Ω .

Hence, to discuss limit cycles of (3.1), we need the assumption that

$$\mu > D \quad \text{and} \quad k > \lambda. \quad (3.3)$$

Then we obtain the necessary and sufficient condition for the existence of a unique limit cycle in Ω . Our main result is the following:

Theorem 3.2. *Suppose that (3.3) holds. If*

$$(D + \mu)\lambda + \frac{bk(\mu - D)}{r\lambda} < Dk, \quad (3.4)$$

then system (3.1) has a unique limit cycle; otherwise it has no limit cycles in Ω .

We remark that parameters satisfying

$$(D + \mu)\lambda + \frac{bk(\mu - D)}{r\lambda} = Dk$$

are bifurcation values. As parameters satisfying condition (3.4) approach the bifurcation values, the unique limit cycle of (3.1) becomes smaller and smaller until reaching the positive equilibrium E^* . Hence, by Theorems 3.1 and 3.2, together with the Poincaré-Bendixson theorem, we have the following:

Corollary 3.1. *Suppose that (3.2) holds. Then the positive equilibrium E^* is globally asymptotically stable if and only if*

$$(D + \mu)\lambda + \frac{bk(\mu - D)}{r\lambda} \geq Dk \quad (3.5)$$

holds.

In Theorem 3.2 and Corollary 3.1, we provide necessary and sufficient conditions on both the uniqueness of limit cycles and the global asymptotic stability of a positive equilibrium for (3.1). These mean that (3.1) has only one limit cycle whenever it exists. A limit cycle emerging from a Hopf bifurcation is kept unique even far from the bifurcation points. Reversing a remark mentioned above, we can say that the limit cycle becomes larger and larger as parameters satisfying (3.4) are farther and farther away from the bifurcation points. Let $\mu > D$ here, which is a reasonable assumption for the maintenance of the predator population.

Suppose that $k \leq \lambda$. Then, without prey immigration, there is no positive equilibrium. In the absence of positive equilibrium, Theorem 1 tells that a boundary equilibrium E_+ not only is stable but also attracts all positive solutions of (3.1) (i.e. E_+ is globally asymptotically stable). As the prey immigration rate b is increased from 0, a positive equilibrium becomes feasible when $\lambda \geq k > r\lambda^2/(r\lambda + b)$ and is ensured by Corollary 3.1 to be always globally asymptotically stable. Constant-rate prey immigration is suggested as a factor which enables species to stably coexist. If we suppose that $k > \lambda$, there is a positive equilibrium even without prey immigration. Without prey immigration, the positive equilibrium is globally asymptotically stable for the case $(D + \mu)\lambda/D \geq k > \lambda$, while a unique limit cycle exists for the case $k > (D + \mu)\lambda/D$. As described above, the increase in k amplifies the amplitude of the fluctuations. As the prey immigration rate b is increased from 0, the positive equilibrium that has been globally asymptotically stable still has the same properties for the former case, while the limit cycle takes both populations farther and farther from zero for the latter case.

A novel aspect of our study is a clear formulation representing the effect of prey immigration by necessary and sufficient conditions derived for both the uniqueness of limit cycles and the global asymptotic stability of a positive equilibrium. In the context of a stabilizing mechanism, our model prediction does not violate the fact that immigration uncoupled from local dynamics is a stabilizing effect on parasitoid-host and predator-prey models (see [5]). Prey immigration introduced here stabilizes/regulates predator-prey populations in a simple framework, promoting equilibrium of the prey population level.

To expand upon this model, the next steps include the consideration of higher trophic level, more general functional responses, roles of other spatial elements, and more general formulations for species immigration (or migration). Developing these considerations will lead to mathematically interesting difficulties that require a wider variety of techniques to resolve. Predator-prey dynamics have been extensively modeled and analyzed in the field of theoretical ecology while simultaneously having numerical considerations on various types of spatially interacting populations (e.g. [13, 20]). However, ample room remains for further exploration from the viewpoint of mathematics. Mathematically rigorous derivations of necessary and sufficient conditions on the unique existence and non-existence of limit cycles for predator-prey populations, such as the present model, will also help to improve our understanding of predator-prey interactions as well as explore solution to the paradox of enrichment.

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